

# Mapping QTLs of root morphological traits at different growth stages in rice

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**Abstract** Roots are a vital organ for absorbing soil moisture and nutrients and influence drought resistance. The identification of quantitative trait loci (QTLs) with molecular markers may allow the estimation of parameters of genetic architecture and improve root traits by molecular marker-assisted selection (MAS). A mapping population of 120 recombinant inbred lines (RILs) derived from a cross between *japonica* upland rice ‘IRAT109’ and paddy rice ‘Yuefu’ was used for mapping QTLs of developmental root traits. All plant material was grown in PVC-pipe. Basal root thickness (BRT), root number (RN), maximum root length (MRL), root fresh weight (RFW), root dry weight (RDW) and root volume (RV) were phenotyped at the seedling (I), tillering (II), heading (III), grain filling (IV)

and mature (V) stages, respectively. Phenotypic correlations showed that BRT was positively correlated to MRL at the majority of stages, but not correlated with RN. MRL was not correlated to RN except at the seedling stage. BRT, MRL and RN were positively correlated to RFW, RDW and RV at all growth stages. QTL analysis was performed using QTLMapper 1.6 to partition the genetic components into additive-effect QTLs, epistatic QTLs and QTL-by-year interactions ( $Q \times E$ ) effect. The results indicated that the additive effects played a major role for BRT, RN and MRL, while for RFW, RDW and RV the epistatic effects showed an important action and  $Q \times E$  effect also played important roles in controlling root traits. A total of 84 additive-effect QTLs and 86 pairs of epistatic QTLs were detected for the six root traits at five stages. Only 12 additive QTLs were expressed in at least two stages. This indicated that the majority of QTLs were developmental stage specific. Two main effect QTLs, *brt9a* and *brt9b*, were detected at the heading stage and explained 19% and 10% of the total phenotypic variation in BRT without any influence from the environment. These QTLs can be used in breeding programs for improving root traits.

Yanying Qu and Ping Mu contributed equally to this study.

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**Keywords** Rice (*Oryza sativa* L.) · Root traits ·  
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## Introduction

With the expansion of global population, the demand for food has dramatically increased. Rice (*Oryza sativa* L.), as one of the most important food sources, is playing and will play a critical role in fulfilling these needs. However, worldwide water shortage will be a challenge for rice production (Clark 1991; Brown and Halwei 1998). The

most effective strategy to manage this problem would be to develop drought resistance cultivars. Prior studies have proven that strong root growth is an important factor in drought resistance (Yoshida and Hasegawa 1982; Ray et al. 1996), especially root length and thickness, which are positively correlated with drought resistance (Ekanayake et al. 1985; Fukai and Cooper 1995; Nguyen et al. 1997; Price and Courtois 1999). Root thickness, root dry weight (RDW), root volume (RV), and root length density are highly heritable traits (Ekanayake et al. 1985; Loresto et al. 1983). These traits are difficult to evaluate in practice since removing intact roots from soil is tedious and root morphological characteristics are complex and easily influenced by environment. Molecular marker-assisted selection may facilitate the development of new cultivars with improved root traits, as well as understanding the genetics of root traits, and cloning the genes using map-based approaches. Since O'Toole (1989) initially selected drought resistance related traits with molecular marker technology, many quantitative trait loci (QTL) for root morphological traits and drought tolerance traits have been identified (Champoux et al. 1995; Yadav et al. 1997; Price and Tomos 1997; Price et al. 2002; Zhang et al. 2001a; Li et al. 2005; Courtois et al. 2000; Kamoshita et al. 2002). Price et al. (1997, 2002) identified several QTLs of root traits within F<sub>2</sub> populations and recombinant inbred (RI) lines derived from *japonica* × *indica* in a hydroponics system and thin soil chamber conditions. With the RI lines from the cross between *indica* × *indica*, Ali et al. (2000) found QTLs underlying five traits related to drought resistance including root penetrability under a condition of paraffin layer simulating a hard pan of soil. Zhang et al. (2001b) reviewed the QTLs and epistasis for controlling seminal root length in suspension-culture and paper-culture environments, which represented a different water supply. These studies confirmed that root traits were controlled by additive and epistatic effects, as well as their QTLs × environment interaction effects. Identification of QTLs underlining root traits were not consistent among experiments and varied in different development stages (Price et al. 2002; Zhang et al. 2001a).

Atchley and Zhu (1997) demonstrated that the genetic mechanism of controlling complex quantitative trait changed distinctly in ontogeny. Conditional QTL mapping may be a valid way to reveal dynamic gene expression for the development of quantitative traits, especially for epistatic effects (Cao and Zhu 2001; Zhu 1995, 1998). Mapping QTL with genetic main effects and QTLs × environment interaction effects could help understand the nature of the quantitative traits (Yan et al. 1998; Hittalmani et al. 2003; Li et al. 2003; Wade 1999).

Previous studies on root traits were mostly conducted in the greenhouse (Price et al. 1997). The methods of soil

chambers and hydroponics under greenhouse conditions played an important role for morphological characterization of root traits, but these methods were insufficient to estimate environment effects on root traits. Most QTLs reported so far have been focused on root morphological characters at a specific or early growth stage. The objective of this research was to identify QTLs underlying root traits of rice at five growing stages using conditional QTL mapping approach.

## Materials and methods

### Plant materials

A population of 120 RI lines derived from a cross between Yuefu (a *japonica* lowland cultivar) and IRAT109 (a *japonica* upland cultivar) was used in this study. IRAT109 is an upland tropical *japonica* rice cultivar from Africa with robust root system, strong shoot, high yield, large seed, and poor grain quality. Yuefu is a lowland temperate *japonica* cultivar from Japan with thin and short root system, high root number and good grain quality which has been extensively grown in Northern China for many years.

### Phenotype

The parents and RI lines were directly seeded in 30 cm diameter PVC pipe in early May of 2003 and 2004 at China Agricultural University, Beijing. The PVC pipes were cut into 80-cm-long segments for tillering stage (II), 100-cm-long segments for heading stage (III), 120-cm-long for filling stage (IV) and 150-cm-long segments for maturity stage (V). Each segment was cut vertically into two halves which were then bound together. The inside-diameter of the pipe segment was 15 cm and a plastic membrane was attached inside. The pipes were buried almost completely underground with only 10 cm above the soil surface and then filled with soil from the rice field. Pipe-culture was conducted as described by Li et al. (2005). Genotypes tested were grown in hill plots. Each pipe contained five hills with a single plant in a hill. Two or three seeds per hill were initially sown and seedlings were thinned after emergence. Paddy soil that mixed a basal fertilizer equivalent to 150 kg/ha N, 150 kg/ha P<sub>2</sub>O<sub>5</sub> and 150 kg/ha K<sub>2</sub>O was filled into the pipe. An additional 300 kg/ha of urea was applied at the tillering stage and filling stage. No water layer was established during the whole growth period. Five supplementary irrigations were provided at seedling emergence, tillering initial stage, tillering prosperity stage, heading stage and grain filling stage, respectively.

The plants were sampled at the seedling stage (after 30 days of emergence), tillering stage (60 days), heading stage (95 days), grain filling stage (112 days), and maturity stage (132 days). The traits were measured on cleaned roots. Five individual plants were evaluated for each genotype for six root traits, basal root thickness (BRT), total root number (RN), maximum root length (MRL), root fresh weight (RFW), RDW and RV. For BRT, root diameter was measured from the upper 1 cm length of the roots under the microscope and the mean value of five thick roots represented the BRT of the plant. For RN, only the first ramification was counted. For MRL, the measurement was taken from the caudexes to the end of root. For RFW, whole fresh roots were simply weighed. For RDW, after deactivating enzymes at 105°C for 10 min, the roots were then dried to constant weight and weighed. For RV, the additional volume was recorded when the entire plant root was immersed into an ethanol filled graduated cylinder.

#### Genotyping and linkage map construction

The tender leaves of 120 RI lines and parental lines were collected for DNA extraction by the CTAB (hexadecyltrimethyl ammonium bromide) method described by Rogers and Bendich (1988). The 520 pairs of SSR primers based on the sequences obtained from Temnykh et al. (2000, 2001) were screened for polymorphism between parental lines. PCR assay was based on the protocol described by McCouch et al. (2001). The linkage map was constructed by the software MAPMAKER/EXP 3.0vol (Lander et al. 1987; Lincoln et al. 1993) with a LOD  $\geq 3.0$ , the recombinant rate  $\leq 0.4$  and the map function was Kosambi. The order of the linkage groups was determined by the COMPARE, MAP, TRY and RIPPLE commands. The commands “compare” and “map” was used to construct a basic linkage

group and the command “try” was used to build a slightly larger group. Given a known map order, “ripple” instructs MAPMAKER to permute the order of neighboring markers, and to compare the likelihoods of the resulting maps.

#### Data analysis

The correlations between different traits at the same developmental stage were analyzed by SPSS (v.11.0). A method of composite interval mapping based on mixed linear model (MCIM) was applied to detect QTLs and to estimate additive effects, epistatic effects and QTLs  $\times$  year ( $Q \times E$ ) interaction effects by QTL Mapper Version 1.6 (Wang et al. 1999). Conditional QTL analysis was conducted with the phenotype at time  $t$ , given the phenotypic behavior at time  $(t-I)$ , using QGA station 1.0 (Zhu 1995). Threshold probability was used for testing likelihood ratio (LR). When the threshold value ( $P \leq 0.005$ ) was determined by the threshold probability setting, the value of LR was 7.8794 (LOD = 1.7098). If a LR value at the peak was above the threshold in the proceeding of two-dimensional search using stepwise regression, the testing point with that LR value was declaring the presence of putative QTL. The significance of the additive and epistatic effects was tested by a  $t$ -test and  $Q \times E$  interaction effects were further tested by a Jackknife test ( $P \leq 0.05$ ). A relative contribution was calculated as the proportion of variance caused by a specific genetic source in the total phenotypic variance, taken as heritability contributed by that genetic source. The general contribution (coefficient of determination) for each genetic source was calculated from the relative contributions of all the putative QTLs involved. The QTLs for which the marker intervals were just the same as their loci were recognized as the same one QTL at different identification. For adjacent QTLs, if the loci with distance below

**Table 1** Correlation coefficients among six studied traits at five growth stages

Traits	Stages				
	I	II	III	IV	V
BRT and RN	0.071	−0.145	−0.234	0.046	0.007
MRL and RN	0.321**	−0.035	−0.063	0.042	−0.103
BRT and MRL	0.404**	0.225*	0.450**	0.348**	0.061
BRT and RFW	0.327**	0.399**	0.264**	0.324**	0.284**
BRT and RDW	0.406**	0.294**	0.502**	0.269**	0.180**
BRT and RV	0.094	0.147	0.463**	0.265**	0.327**
MRL and RFW	0.495**	0.410**	0.348**	0.526**	0.318**
MRL and RDW	0.382**	0.417**	0.222*	0.370**	0.214*
MRL and RV	0.392**	0.285**	0.352**	0.368**	0.279**
RN and RFW	0.626**	0.237**	0.434**	0.520**	0.532**
RN and RDW	0.416**	0.292**	0.589**	0.667**	0.524**
RN and RV	0.672**	0.237**	0.280**	0.518**	0.338**

\*, \*\*—significant at 0.05 and 0.01 possibility level

5 cM were specified as the same QTL, then its effecting value adopted its mean value.

## Results

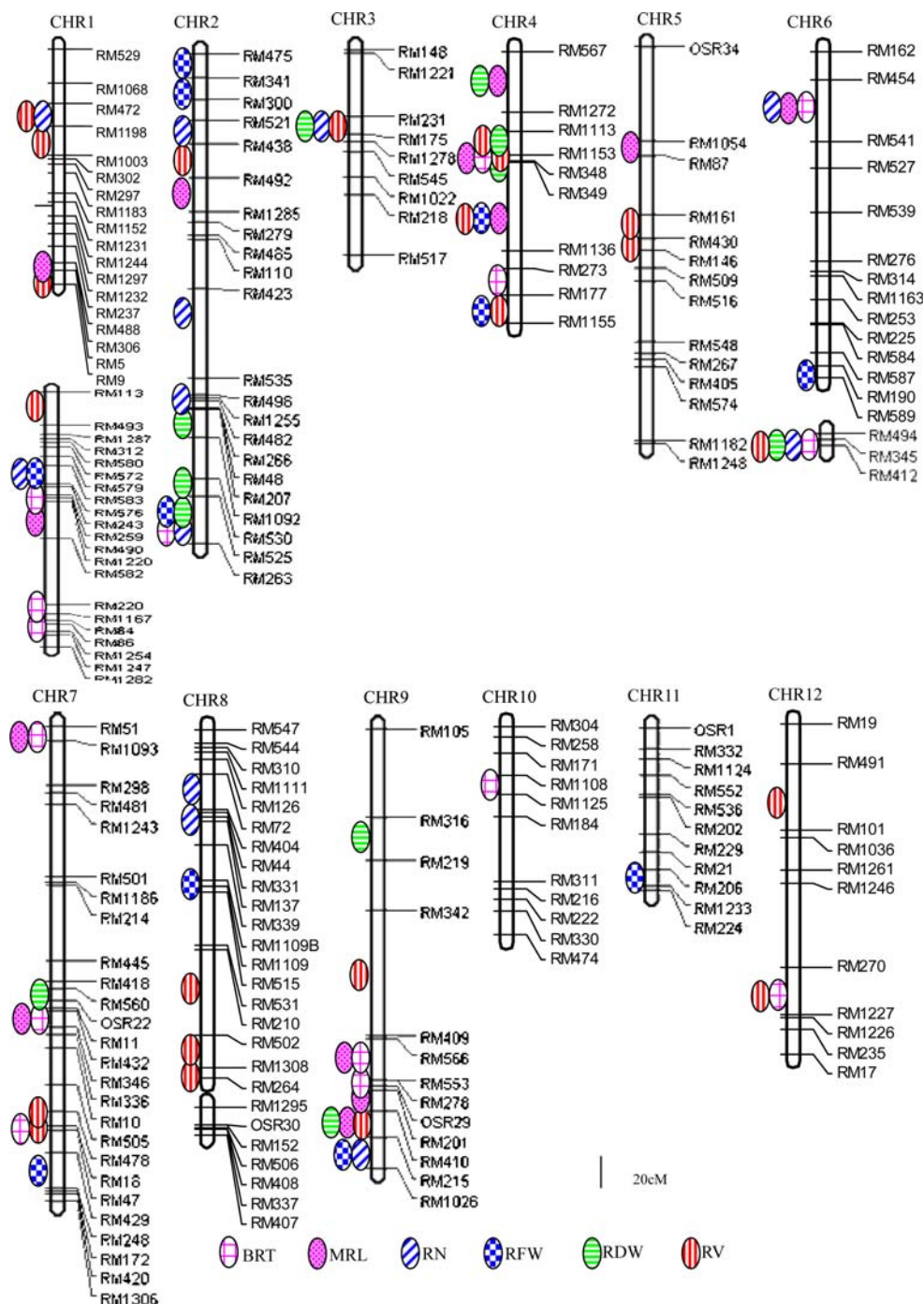
The value and correlations of root morphological characteristics

Based on the root trait investigations, it was found that IRAT109 had significantly larger value than Yuefu in

2004, except for RN in 2003 (Supplemental Table 1). The variation of the RIL population in 2004 was greater than that in 2003 and the distributions of phenotypic characteristics tended to be normal (test of normality). We also found a transgressive segregation for six traits in two years.

The correlation coefficients ( $r$ ) between the traits and different stages were calculated from the mean value of two years data (Table 1). MRL had no significant correlation with RN except at the seedling stage. BRT had no

**Fig. 1** Additive QTLs for root trait of RI population



correlation with RN through all stages, but BRT had a significant positive correlation with MRL from seedling to filling, and no significant correlation at the maturity stage. BRT, MRL and RN showed a significant positive correlation with RFW and RDW at all growth stages ( $P < 0.01$ ). The correlation results in this study were identical to the results by Hirawasa (1999) and Mu et al. (2003). BRT and MRL, related to drought resistance (Li et al. 2005), were also highly correlated in this study and either can be used to improve root traits for drought resistance in rice.

### Linkage map

Of the 520 SSR markers, 216 were polymorphic with a polymorphism rate of 41%. This rate was higher than those of other intra-subspecies populations (17% between two *indica* parents, Ali et al. 2000), because the parents were from geographically distant regions. 201 SSR markers were integrated into 15 linkage groups covering 1833 cM in all 12 chromosomes with an average distance of 9.0 cM between adjacent markers. Due to insufficient polymorphic markers between gaps, chromosomes 1, 2 and 8 were separated into two linkage groups (Fig. 1). This linkage map was in accordance with the rice molecular marker linkage maps of previous authors (McCouch et al. 2002, Temnykh et al. 2000). The genome coverage was estimated to be approximately 90% on the basis of the two saturated maps mentioned above.

### QTLs analysis

The advantage of QTL mapping approaches using QTL Mapper Version 1.6 is when simultaneously dealing QTL

with complicated epistasis effect and  $Q \times E$  effects, so that it provides a powerful tool for geneticists and breeders to further analyze the interaction between QTL and environment.

In this study, 84 additive effect QTLs and 86 pairs of epistatic QTLs were identified for six traits at five stages and the QTLs were distributed on all 12 chromosomes of rice. Only 12 additive QTLs were consistently identified at two or more different stages (Table 2) which indicated that the majority QTLs were developmental stage specific.

### BRT

Fourteen additive QTLs affecting BRT during the whole growth period were detected. Eleven of 14 alleles with positive effects came from IRAT109 which could account for 79% of total additive QTLs. Three (brt6a, brt4b, and brt6b) of the 14 QTLs were identified at two different stages (Table 3). A total of 11 pairs of epistatic QTLs were identified in all stages, except at the seedling stage (Table 3). Two QTLs, brt9a and brt9b, had significant additive main effects (0.07, 0.05) at the heading stage which could explain 19% and 10.7% of the phenotypic variation respectively and the favorable alleles were contributed by IRAT109. For BRT, additive QTLs contributions accounted for the total different effects, and the QTLs contributions were about 0.393, 0.374, 0.960, 0.108, and 0.196 at stages I, II, III, IV, and V, respectively. Therefore it was concluded that additive effects were a big contributor to BRT at different stage except at the filling stage (Fig. 2).  $Q \times E$  interaction effect was another important factor. However, no  $Q \times E$  effect was found at the heading stage in this study.

**Table 2** additive QTLs of consistent expression at two or more different stages

Traits	Interval	LOD value				
		I	II	III	IV	V
BRT	RM454-RM541	5.10				4.13
	RM1153-RM348		10.40			13.00
	RM345-RM412				7.89	8.04
RN	RM231-RM175			10.30		7.37
MRL	RM567-RM1272	8.68	4.74	4.32	6.21	
	RM201-RM410		7.51	4.73	7.38	9.48
RFW	RM349-RM1136			4.32		14.70
RV	RM18-RM47	5.01			5.39	
	RM491-RM101	5.67				4.32
	RM1198-RM1003		4.85	4.63		
	RM345-RM412		5.38			4.51
	RM1308-RM264				7.97	5.43

**Table 3** QTLs associated with BRT in the IRAT109/Yuefu RIL population at five stages

St <sup>f</sup>	QTL <sup>a</sup>	Int. Name <sub>i</sub>	Site <sub>i</sub> (M) <sup>g</sup>	QTL <sup>a</sup>	Int. Name <sub>j</sub>	Site <sub>j</sub> (M)	LOD	a <sub>i</sub> <sup>b</sup>	a <sub>j</sub> <sup>b</sup>	aa <sub>ij</sub> <sup>c</sup>	ae <sub>i</sub> <sup>d</sup>	ae <sub>j</sub> <sup>d</sup>	aae <sub>ij</sub> <sup>e</sup>
I	brt1a	RM220-RM1167	0.00	brt1b	RM86-RM1254	0.00	9.42	-0.02	0.01		-0.02	-0.01	
	brt4a	RM273-RM177	0.12	brt8-1	RM407-RM337	0.00	17.17	0.06			0.06		
	brt6a	RM454-RM541	0.28	brt6-6	RM276-RM314	0.00	5.58	0.05			-0.03		
II	brt1-1	RM529-RM1068	0.06	brt6-1	RM162-RM454	0.14	5.09			0.04			0.03
	brt1c	RM490-RM1220	0.00	brt2-21	RM525-RM263	0.30	4.44	0.03			-0.02		
	brt1c	RM490-RM1220	0.02	brt6-16	RM345-RM412	0.00	4.30	0.02			-0.02		
	brt1c	RM490-RM1220	0.02	brt8-1	RM407-RM337	0.00	6.58	0.03		-0.03			-0.02
	brt4-1	RM567-RM1272	0.22	brt7a	RM432-RM346	0.00	4.67		0.03	-0.04			-0.03
	brt4b	RM1153-RM348	0.00	brt4-8	RM273-RM177	0.12	10.39	0.04			-0.05		
	brt10	RM1108-RM1125	0.02	brt10-5	RM311-RM216	0.02	4.28	0.03					
	brt5-9	RM548-RM267	0.00	brt8-19	RM1109B-RM1109	0.02	5.87			-0.03			
III	brt7a	RM51-RM1093	0.00	brt7-4	RM481-RM1243	0.06	7.24	0.04			0.02		
	brt9a	RM566-RM553	0.22	brt9-10	RM201-RM410	0.12	8.31	0.07					
	brt9b	RM278-OSR29	0.02	brt9-11	RM410-RM215	0.16	7.27	0.04					
	brt1-19	RM577-RM113	0.48	brt12	RM270-RM1227	0.00	8.08		-0.03	-0.06			-0.04
IV	brt4-1	RM567-RM1272	0.00	brt8-16	RM331-RM137	0.00	6.67			0.05			0.05
	brt5-6	RM146-RM509	0.04	brt12-8	RM1227-RM1226	0.00	4.39			-0.03			-0.04
	brt6a	RM345-RM412	0.00	brt7-2	RM1093-RM298	0.00	7.89	-0.04			0.04		
	brt7-25	RM420-RM1306	0.02	brt10-5	RM311-RM216	0.00	4.91			-0.03			-0.04
	brt1-39	RM1247-RM1282	0.06	brt6b	RM345-RM412	0.00	8.00		0.03			-0.02	
V	brt2	RM525-RM263	0.20	brt3-4	RM175-RM1278	0.00	14.74	0.04			-0.05		
	brt4b	RM1153-RM348	0.02	brt4-7	RM1136-RM273	0.02	12.98	0.05			-0.03		
	brt4b	RM1153-RM348	0.02	brt4-9	RM177-RM1155	0.00	10.75	0.05			-0.03		
	brt4-6	RM349-RM1136	0.40	brt8-12	RM126-RM72	0.06	9.15			0.03			0.04
	brt5-9	RM548-RM267	0.06	brt7-15	RM346-RM336	0.02	7.24			-0.04			-0.03
	brt5-12	RM574-RM1182	0.54	brt6a	RM454-RM541	0.02	6.17		0.03		0.03	-0.02	
	brt6a	RM454-RM541	0.00	brt6-6	RM276-RM314	0.00	4.13	0.02					0.01
	brt6b	RM345-RM412	0.00	brt7-2	RM1093-RM298	0.22	8.04	0.03			-0.02		
	brt7-20	RM18-RM47	0.00	brt11-3	RM1124-RM552	0.02	9.05			-0.04			-0.03

<sup>a</sup> QTLs are denoted by trait abbreviations plus chromosomal number

<sup>b</sup> “a<sub>i</sub>”, “a<sub>j</sub>” is the additive effect of a QTL<sub>i</sub> and a QTL<sub>j</sub>, respectively. A positive value indicates that the IRAT 109 genotype has a positive effect on the trait

<sup>c</sup> “aa<sub>ij</sub>” is the additive × additive effect QTLs interaction

<sup>d</sup> “ae<sub>i</sub>”, “ae<sub>j</sub>” is the additive effect QTL<sub>i</sub> and QTL<sub>j</sub> interaction with year, respectively

<sup>e</sup> “aae<sub>ij</sub>” is the epistatic effect QTLs interaction with year

<sup>f</sup> “st” is developmental stages, seedling(I), tillering(II), heading(III), grain filling stage(IV) and mature (V) stages, respectively

<sup>g</sup> is the number of left marker involve a QTL

## RN

Thirteen additive QTLs were identified at different developmental stages except at the seedling stage (Table 4). Yuefu contributed most alleles for increasing root number (accounted for 71% of total additive QTLs). Of these 13 QTLs, only rn3 was consistently present at heading and maturity stages. A total of 15 pairs of epistatic QTLs were identified in all stages, except at the seedling stage (Table 4). Analysis of the effect components of each QTL

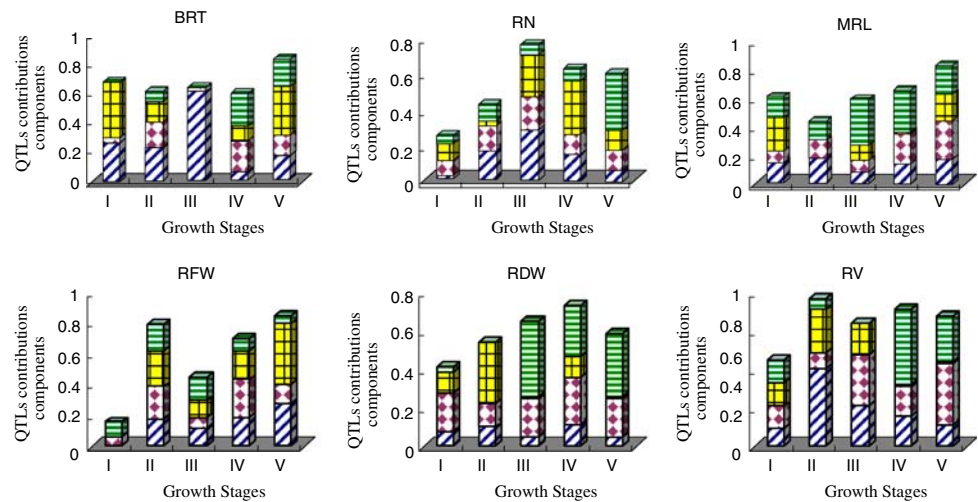
showed that RN was affected by additive effect at all developmental stages except maturity (Fig. 2) and effects from Q × E became important after the tillering stage.

## MRL

Fourteen additive QTLs underlying MRL were identified for the whole growth period (Table 5) however, only mrl4a and mrl9a could be detected at the four stages. The QTL

**Fig. 2** General contributions (coefficient of determination; 1 = 100%) of different effects for root traits at different stages

■: additive QTLs contributions;  
 ■: epistatic QTLs contributions;  
 ■: additive × year QTLs contributions;  
 ■: epistatic × year QTLs contributions



**Table 4** QTLs associated with RN in the IRAT109/Yuefu RIL population at five stages

st	QTL	Int. Namei	Sitei (M)	QTL	Int. Namej	Sitej (M)	LOD	$a_i$	$a_j$	$aa_{ij}$	$ae_i$	$ae_j$	$aae_{ij}$
I	rn1-7	RM297-RM1183	0.02	rn1-16	RM306-RM5	0.00	4.70			-0.95			
II	rn1-35	RM1167-RM84	0.04	rn5-8	RM516-RM548	0.44	4.35			1.91			2.89
	rn2a	RM521-RM438	0.00	rn2-8	RM279-RM485	0.00	5.69	3.04			2.11		
	rn2b	RM423-RM535	0.00	rn2c	RM1255-RM482	0.00	6.73		-2.46			-2.20	
	rn2b	RM423-RM535	0.16	rn10-1	RM171-RM1108	0.06	4.99	-2.65			3.41		
	rn2c	RM1255-RM482	0.00	rn6-5	RM539-RM276	0.00	6.12	-2.98			-2.05		
	rn5	RM1182-RM1248	0.00	rn7-19	RM478-RM18	0.06	4.04	-1.60		-2.69	3.07		
	rn9-3	RM219-RM342	0.16	rn9-6	RM566-RM553	0.04	4.10			3.07			2.54
III	rn1a	RM472-RM1198	0.14	rn1-4	RM1183-RM1152	0.00	7.65	4.99			-4.74		
	rn1-12	RM1297-RM1232	0.04	rn9-6	RM566-RM553	0.26	6.20			4.44			-3.39
	rn1-25	RM572-RM579	0.02	rn5-3	RM87-RM161	0.34	4.33			-4.73			-3.99
	rn1b	RM583-RM576	0.00	rn1-30	RM259-RM490	0.00	5.25	-3.95		3.28	-3.16		
	rn3	RM231-RM175	0.00	rn3-6	RM545-RM1022	0.00	10.28	-7.96			4.08		-3.27
	rn6a	RM454-RM541	0.04	rn9-2	RM316-RM219	0.02	7.76	-4.94		-4.50			4.48
IV	rn6a	RM454-RM541	0.12	rn6b	RM345-RM412	0.00	6.90		-5.88	8.28		-6.83	6.19
	rn6-6	RM276-RM314	0.00	rn10-2	RM1108-RM1125	0.08	5.67			5.34			6.21
	rn6b	RM345-RM412	0.02	rn9-5	RM409-RM566	0.00	6.43	-6.56		-5.28	-5.20		-5.12
	rn8a	RM72-RM404	0.16	rn8b	RM331-RM137	0.02	7.07	9.60	-12.53	-7.68			
	rn8b	RM331-RM137	0.00	rn8-19	RM1109B-RM1109	0.00	9.00	-5.45			9.27		
	rn9	RM215-RM1026	0.00	rn10-3	RM1125-RM184	0.10	9.27	7.85			-8.13		
V	rn1-1	RM529-RM1068	0.08	rn1-22	RM1287-RM312	0.02	4.05			4.99			5.05
	rn1-27	RM583-RM576	0.02	rn9-10	RM201-RM410	0.00	5.21			5.49			-5.79
	rn2-17	RM48-RM207	0.00	rn7-8	RM214-RM445	0.38	6.50			-6.04			6.06
	rn2d	RM525-RM263	0.06	rn3	RM231-RM175	0.02	8.49	5.33	-5.68			7.565	
	rn3	RM231-RM175	0.04	rn3-6	RM545-RM1022	0.00	7.37	-7.14			7.44		

mrl9a had a major significant additive effect at tillering stage (2.27) and maturity stage (8.63). A total of 10 pairs of epistatic QTLs were identified at all stages (Table 5). For MRL, additive effects played a more important role before the filling stage, after which epistatic effects became more pronounced (Fig. 2).

#### RFW

There were 11 additive QTLs detected for RFW at all development stages except at the seedling stage (Table 6). The QTL rfw4 was found at two stages. A total of 14 pairs of epistatic QTLs were identified at all growth stages

**Table 5** QTLs associated with MRL in the IRAT109/Yuefu RIL population at five stages

st	QTL	Int. Namei	Sitei (M)	QTL	Int. Namej	Sitej (M)	LOD	a <sub>i</sub>	a <sub>j</sub>	aa <sub>ij</sub>	ae <sub>i</sub>	ae <sub>j</sub>	aae <sub>ij</sub>
I	mrl1a	RM1220-RM582	0.18	mrl1-37	RM86-RM1254	0.00	11.29	1.49			–1.33		
	mrl2	RM492-RM1285	0.04	mrl2-9	RM485-RM110	0.00	11.61	–1.46			0.88		
	mrl4a	RM567-RM1272	0.00	mrl4-5	RM348-RM349	0.00	8.68	–0.59			0.59		
	mrl6	RM454-RM541	0.30	mrl8-14	RM404-RM44	0.00	8.02	1.15			–1.85		
	mrl6	RM454-RM541	0.30	mrl6-6	RM276-RM314	0.00	7.44	0.93			–1.24		
	mrl6-12	RM587-RM190	0.04	mrl12-4	RM1036-RM1261	0.16	9.50			1.02			–1.20
II	mrl1-20	RM113-RM493	0.08	mrl7-21	RM47-RM429	0.00	6.42			2.17			2.47
	mrl1b	RM1167-RM84	0.04	mrl7-21	RM47-RM429	0.10	7.10	1.35		–2.24			–2.02
	mrl2-1	RM475-RM341	0.00	mrl9a	RM201-RM410	0.08	7.76		2.83			1.81	
	mrl4a	RM567-RM1272	0.02	mrl4b	RM349-RM1136	0.48	4.74	2.13			1.68		
	mrl9a	RM201-RM410	0.12	mrl10-1	RM171-RM1108	0.10	7.51	2.69			1.79		
III	mrl1-18	RM9-RM577	0.56	mrl2-5	RM438-RM492	0.20	7.42			2.52			–4.22
	mrl4a	RM567-RM1272	0.00	mrl5-10	RM267-RM405	0.02	4.32	–0.90		2.49			–1.61
	mrl7a	RM51-RM1093	0.00	mrl8-7	RM1295-RM547	0.38	7.57	3.95			–2.87		
	mrl9a	RM201-RM410	0.08	mrl10-1	RM171-RM1108	0.00	4.73	1.28			–3.39	1.87	
IV	mrl1-34	RM220-RM1167	0.04	mrl8-16	RM331-RM137	0.00	4.10			–3.81			3.38
	mrl1-39	RM1247-RM1282	0.02	mrl4c	RM1153-RM348	0.00	8.71		2.26		–2.66	1.57	4.72
	mrl4a	RM567-RM1272	0.06	mrl4-5	RM348-RM349	0.00	6.21	0.32		–3.48			4.69
	mrl4c	RM1153-RM348	0.02	mrl9a	RM201-RM410	0.10	7.29	2.06	1.95				
	mrl4b	RM349-RM1136	0.18	mrl9	RM410-RM215	0.08	8.13	5.27	4.08		–3.95	–4.00	
	mrl5-10	RM267-RM405	0.00	mrl12-4	RM1036-RM1261	0.04	5.79			–4.09			3.64
	mrl6-3	RM541-RM527	0.12	mrl9-5	RM409-RM566	0.00	5.08			–4.43			4.49
V	mrl1c	RM306-RM5	0.00	mrl1-19	RM577-RM113	0.22	15.75	5.90			–6.87		
	mrl5	RM1054-RM87	0.10	mrl5-6	RM146-RM509	0.12	11.98	–4.74			4.31		
	mrl7b	RM432-RM346	0.06	mrl8-6	OSR30-RM1295	0.08	6.64	2.76			2.42		
	mrl9b	RM566-RM553	0.26	mrl9a	RM201-RM410	0.04	9.48	–3.59	8.82	–7.14		–5.06	5.65

(Table 6). No additive effects were observed for RFW at the seedling stage. For RFW, epistatic effect played an important role at all stages. There was a great amount of  $Q \times E$  effect at the tillering and maturity stages (Fig. 2).

### RDW

Twelve additive QTLs were detected during the growth period (Table 7). None were consistently presented at different stages. A total of 17 pairs of epistatic QTLs were identified in all stages (Table 7). RDW was mainly affected by epistatic effects. The effect from  $Q \times E$  played an important role during all growth stages (Fig. 2).

### RV

Twenty two additive QTLs during the whole developmental period were identified (Table 8), of which rv1b, rv7a, rv12a and rv6 could be detected at two different

stages. Nineteen pairs of epistatic QTLs were found at all stages (Table 8). Generally, additive effects were involved at early growth stages and epistatic effects showed up at late growth stages (Fig. 2).

### Discussion

The relation between root traits and drought resistance has been highlighted for a long time, and the previous QTL-mapping studies on root traits of rice were set only on one or a few early growth stages (Price et al. 1997, 2002; Champoux et al. 1995; Zhang et al. 2001b; Xu et al. 2004; Li et al. 2005; Kamoshita et al. 2002). However, QTL-mapping related to root traits with drought tolerance for developmental behavior at all developmental stages and the interactions between QTLs and environment under field growing conditions has not been reported. In the present study, the RILs derived from the cross of IRAT109  $\times$  Yuefu were used to reveal the mechanism of development genetics for root traits in rice.

**Table 6** QTLs associated with RFW in the IRAT109/Yuefu RIL population at five stages

st	QTL	Int. Namei	Sitei (M)	QTL	Int. Namej	Sitej (M)	LOD	a <sub>i</sub>	a <sub>j</sub>	aa <sub>ij</sub>	ae <sub>i</sub>	ae <sub>j</sub>	aae <sub>ij</sub>
I	r fw1-2	RM1068-RM472	0.12	r fw11-6	RM202-RM229	0.02	6.13			0.03			0.04
	r fw1-14	RM237-RM488	0.04	r fw1-22	RM1287-RM312	0.00	6.16			−0.04			−0.03
	r fw4-2	RM1272-RM1113	0.00	r fw4-8	RM273-RM177	0.12	4.71			0.04			0.04
II	r fw2a	RM475-RM341	0.00	r fw3-1	RM148-RM1221	0.00	11.18	0.41			−0.29		
	r fw2a	RM475-RM341	0.04	r fw12-5	RM1261-RM1246	0.00	9.82	0.42			−0.29		
	r fw2b	RM341-RM300	0.14	r fw5-10	RM267-RM405	0.02	9.70	0.39			0.25		
	r fw5-2	RM1054-RM87	0.06	r fw12-1	RM19-RM491	0.18	5.21			−0.31			−0.21
	r fw6-10	RM225-RM584	0.00	r fw7-14	RM432-RM346	0.02	5.92			−0.25			0.24
	r fw6-13	RM190-RM589	0.06	r fw8-20	RM1109-RM515	0.02	6.64			−0.31			−0.21
	r fw8-17	RM137-RM339	0.04	r w11-6	RM202-RM229	0.00	4.41			−0.28			
	r fw11	RM206-RM1233	0.00	r fw12-1	RM19-RM491	0.00	10.22	0.33			−0.46		
III	r fw2c	RM525-RM263	0.30	r fw4-3	RM1113-RM1153	0.10	4.38	−0.87					
	r fw2c	RM525-RM263	0.30	r fw3-4	RM175-RM1278	0.00	6.54	−0.72					
	r fw4a	RM349-RM1136	0.24	r fw5-1	OSR34-RM1054	0.32	4.32	0.72			0.74		
	r fw5-12	RM574-RM1182	0.00	r fw6-4	RM527-RM539	0.20	7.73			0.81			0.90
IV	r fw1-19	RM577-RM113	0.44	r fw2-19	RM1092-RM530	0.20	5.46			1.21			
	r fw2-5	RM438-RM492	0.20	r fw5-2	RM1054-RM87	0.06	5.50			1.08			
	r fw2-12	RM535-RM498	0.00	r fw10-4	RM184-RM311	0.00	4.25			−0.86			0.71
	r fw4b	RM177-RM1155	0.02	r fw6-12	RM587-RM190	0.04	5.75	0.54		−0.90	−0.54		−0.75
	r fw7-23	RM248-RM172	0.00	r fw9	RM215-RM1026	0.00	12.42		1.49			1.19	
	r fw8	RM1109B-RM1109	0.02	r fw8-23	RM210-RM502	0.00	9.22	1.03			−1.28		
	r fw9	RM215-RM1026	0.00	r fw10-2	RM1108-RM1125	0.00	12.63	1.29			1.15		
	r fw10-4	RM184-RM311	0.06	r fw12-6	RM1246-RM270	1.02	4.56			0.98			−0.75
V	r fw1	RM583-RM576	0.02	r fw1-31	RM490-RM1220	0.02	8.68	0.97			−0.72		
	r fw4a	RM349-RM1136	0.00	r fw4-9	RM177-RM1155	0.14	14.74	1.06			0.81		
	r fw6	RM587-RM190	0.06	r fw6-16	RM345-RM412	0.02	15.77	−1.00			−1.24		
	r fw7-1	RM51-RM1093	0.04	r fw12-2	RM491-RM101	0.14	4.37			0.79			
	r fw7	RM429-RM248	0.00	r fw7-25	RM420-RM1306	0.00	4.24	0.54			−0.72		

### Development genetics characteristic of root traits

Based on the total QTL contributive rate of each effect at different stages, we found that the genetic architecture of root traits varied in the different developmental stages with different traits. As a whole, the additive effects played a major role at the majority of the developmental stages for BRT, RN, and MRL, and epistatic effects were the most important ones at all developmental stages for RFW, RDW, and RV (Fig. 2). The fact that for MRL at the seedling stage, the additive effect is an important genetic effect diverges from earlier reports that the epistatic effect is the main effect at the early stage of MRL (Zhang et al. 2001b; Price et al. 1997; Yadav et al. 1997).

In addition, the QTLs  $\times$  environment interaction effects should not be overlooked. Higher contribution rates from Q $\times$ E effects were obtained at different stages except the heading stage with a small interaction. This means that root QTLs were largely affected by environment. The results

above were similar to prior studies that showed that different experiments gave different patterns of QTLs, pointing out to Q  $\times$  E interactions and from which it could be concluded that the genetic model of root growth is complex (Price et al. 2002; Li et al. 2005; Zhang et al. 2001b; Kamoshita et al. 2002).

Some interesting results were that in our study some QTLs which had major additive effects and high contribution were comparatively stable and could be detected under different environments and different populations. The QTL *brt9a* (RM566–RM553) at heading stage was very close to the QTLs (G385, G1085) at maturity stage in the Bala/Azuna (Price et al. 2002), and the QTL (RZ12) at seedling stage in the CO39/Moroberekan (Champoux et al. 1995) and IR64/Az (Yadav et al. 1997; Hemamalini et al. 2000; Zhang et al. 2001a). What is more, two out of three additive QTLs (RM18–RM47, RM1124–RM552) for BRT at the maturity stage were also found very consistent with the QTLs (RM47–RM172, OSR1–RM202) of Li et al.

**Table 7** QTLs associated with RDW in the IRAT109/Yuefu RIL population at five stages

st	QTL	Int. Name <sub>i</sub>	Site <sub>i</sub> (M)	QTL	Int. Name <sub>j</sub>	Site <sub>j</sub> (M)	LOD	a <sub>i</sub>	a <sub>j</sub>	aa <sub>ij</sub>	ae <sub>i</sub>	ae <sub>j</sub>	aae <sub>ij</sub>
I	rdw1-25	RM572-RM579	0.04	rdw7	RM560-OSR22	0.04	4.20		0.006			0.004	0.005
	rdw2a	RM207-RM1092	0.02	rdw7-3	RM298-RM481	0.02	5.95	−0.004			−0.006		
	rdw7	RM560-OSR22	0.00	rdw11-8	RM21-RM206	0.08	6.53	0.004					
	rdw9-11	RM410-RM215	0.14	rdw11-2	RM332-RM1124	0.08	6.85			0.006			−0.005
II	rdw1-31	RM490-RM1220	0.00	rdw6-5	RM539-RM276	0.02	4.85			0.075			0.057
	rdw1-38	RM1254-RM1247	0.00	rdw7-22	RM429-RM248	0.00	4.66			0.047			
	rdw2b	RM530-RM525	0.10	rdw7-9	RM445-RM418	0.00	5.02	−0.039			−0.051		
	rdw4a	RM567-RM1272	0.30	rdw4b	RM348-RM349	0.00	4.82	−0.050	0.039			−0.079	
	rdw9a	RM316-RM219	0.04	rdw9-5	RM409-RM566	0.02	6.08	−0.059			0.060		
III	rdw1-18	RM9-RM577	0.78	rdw3a	RM175-RM1278	0.00	4.51		0.159				
	rdw1-26	RM579-RM583	0.00	rdw8-2	RM337-RM408	0.00	4.71			−0.117			−0.144
	rdw2c	RM525-RM263	0.30	rdw3a	RM175-RM1278	0.00	5.53	0.120	0.124		0.064		
	rdw3-1	RM148-RM1221	0.00	rdw6-4	RM527-RM539	0.22	5.40			−0.206			
	rdw3-3	RM231-RM175	0.00	rdw8-10	RM310-RM1111	0.00	4.69			−0.170			−0.301
	rdw5-12	RM574-RM1182	0.00	rdw6-4	RM527-RM539	0.10	4.56			−0.211			
	rdw6-2	RM454-RM541	0.00	rdw6	RM345-RM412	0.02	5.21			−0.191			
IV	rdw1-18	RM9-RM577	0.00	rdw4-6	RM349-RM1136	0.08	7.18			0.217	−0.176		−0.241
	rdw1-18	RM9-RM577	0.00	rdw12-2	RM491-RM101	0.06	7.58			−0.307	−0.156		
	rdw1-31	RM490-RM1220	0.02	rdw8-2	RM337-RM408	0.00	5.64			0.211			−0.150
	rdw2-12	RM535-RM498	0.06	rdw6-1	RM162-RM454	0.00	4.88			0.205			
	rdw4c	RM1113-RM1153	0.06	rdw5-6	RM146-RM509	0.12	4.61	−0.220					−0.234
	rdw4-7	RM1136-RM273	0.08	rdw6-7	RM314-RM1163	0.00	5.43			0.243			
	rdw6-2	RM454-RM541	0.02	rdw6	RM345-RM412	0.00	9.37		0.207	0.212		0.156	0.301
	rdw7-7	RM1186-RM214	0.00	rdw8-24	RM502-RM1308	0.16	5.57			0.155			0.274
	rdw9b	RM410-RM215	0.14	rdw10-2	RM1108-RM1125	0.06	10.33	−0.250			0.339		
V	rdw1-39	RM1247-RM1282	0.02	rdw2-19	RM1092-RM530	0.18	6.34			0.139			0.199
	rdw2-18	RM207-RM1092	0.16	rdw9-5	RM409-RM566	0.02	4.40			−0.143			
	rdw3b	RM1278-RM545	0.00	rdw3-8	RM218-RM517	0.00	6.74	0.110					

(2005) under upland culture condition. This demonstrated that common QTLs can be detected under different conditions of populations and experimental environments.

#### Selective expression of root traits QTLs at different stages

Different QTLs could be detected at different stages, but only a few common QTLs were detected in all stages (Price and Tomos 1997; Xu et al. 2004; Yan et al. 1998; Wu et al. 1999). By comparing to the QTLs at the stages of 30 day and 40 day after seedling, Xu et al. (2004) found that only one out of seven QTLs was common at both stages for MRL.

However, previous genetic analysis about developmental traits used to treat the phenotypic values as different time points as repeated measurements of the same trait and to analyze the trait under the repeated measurements

framework. The QTL effect of time ( $t-1$ ) on one locus explained accumulation effect of gene expressive from time ( $t$ ) to time ( $t-1$ ), and it was incapable to show the net genetic effect at a special developmental stage with the unconditional QTLs-mapping method. Zhu (1995) described the conditional genetic analysis method through managing an experiment for cotton fruiting data to compare unconditional with conditional genetic variances and additive effects. He indicated that analysis of conditional QTL will provide a way for exploring QTLs expression on quantitative traits in different developmental stages. This method had been used for researching the development behavior of fruiting data in cotton (Zhu 1995), plant height in rice (Cao and Zhu 2001), and body weight and tail length in mice (Atchley and Zhu 1997).

In the present experiment, 12 of 84 additive QTLs were persistently expressed at two or more stages with a percentage of 14.3%, although no QTLs were detected at all stages. The results suggested that the QTLs for root traits

**Table 8** QTLs associated with RV in the IRAT109/Yuefu RIL population at five stages

st	QTL	Int.Namei	Sitei (M)	QTL	Int. Namej	Sitej (M)	LOD	ai	aj	aaij	aei	aej	aaejj
I	rv1-35	RM1167-RM84	0.00	rv4b	RM349-RM1136	0.10	4.99		−0.03				
	rv2-21	RM525-RM263	0.30	rv11-6	RM202-RM229	0.02	8.88			0.05			0.05
	rv4a	RM1153-RM348	0.00	rv6-8	RM1163-RM253	0.00	6.18	−0.03					
	rv5-3	RM87-RM161	0.22	rv12a	RM491-RM101	0.06	5.76		0.05			−0.04	
	rv7a	RM18-RM47	0.00	rv7-23	RM248-RM172	0.00	5.01	−0.02			0.04		
	rv12-2	RM491-RM101	0.04	rv12-5	RM1261-RM1246	0.06	5.64	0.04			−0.04		
II	rv1a	RM472-RM1198	0.12	rv1-7	RM297-RM1183	0.00	6.02	−0.22					
	rv1b	RM1198-RM1003	0.06	rv12-6	RM1246-RM270	0.00	4.85	−0.25					
	rv1c	RM113-RM493	0.00	rv1-23	RM312-RM580	0.00	8.98	0.32			0.29		
	rv1-32	RM1220-RM582	0.04	rv12-5	RM1261-RM1246	0.06	6.25			0.39			
	rv2-17	RM48-RM207	0.00	rv7-7	RM1186-RM214	0.00	5.66					−0.27	
	rv4c	RM177-RM1155	0.14	rv5b	RM161-RM430	0.16	4.33	0.29	−0.42				
	rv5a	RM1054-RM87	0.10	rv9a	RM342-RM409	0.02	4.90		−0.40				
	rv5-5	RM430-RM146	0.00	rv5-8	RM516-RM548	0.20	4.67	−0.36					
	rv6	RM345-RM412	0.02	rv7-3	RM478-RM18	0.00	5.38	−0.46					
	rv8a	RM210-RM502	0.42	rv9-1	RM105-RM316	0.00	6.75	−0.43					
	rv12-3	RM101-RM1036	0.00	rv12-6	RM1246-RM270	1.02	5.42			0.34			
	rv12-4	RM1036-RM1261	0.16	rv12b	RM270-RM1227	0.24	7.33		−0.19			−0.21	
III	rv1	RM1198-RM1003	0.00	rv1-7	RM297-RM1183	0.00	4.63	0.60			−0.92		
	rv1-9	RM1152-RM1231	0.04	rv1d	RM5-RM9	0.10	5.15		0.66	−0.73			0.57
	rv1-10	RM1231-RM1244	0.04	rv11-9	RM206-RM1233	0.04	4.32			0.89			−0.79
	rv1-27	RM583-RM576	0.10	rv8-7	RM1295-RM547	0.34	4.24			−0.99			0.94
	rv1-28	RM576-RM243	0.02	rv4d	RM1113-RM1153	0.00	6.99		1.18			0.66	
	rv2	RM438-RM492	0.08	rv5-10	RM267-RM405	0.02	4.19	−0.93					
	rv2	RM438-RM492	0.16	rv8-13	RM72-RM404	0.04	6.95	−0.79		1.10			−0.67
	rv3	RM231-RM175	0.04	rv3-7	RM1022-RM218	0.02	4.28	−1.09			−0.92		
	rv3-5	RM1278-RM545	0.04	rv12-5	RM1261-RM1246	0.02	4.41			1.11			
	rv3-8	RM218-RM517	0.18	rv4d	RM1113-RM1153	0.00	5.19		1.14			0.60	
IV	rv8b	RM502-RM1308	0.02	rv9-1	RM105-RM316	0.00	4.75	0.70			0.89		
	rv1-17	RM5-RM9	0.04	rv10-1	RM171-RM1108	0.00	7.14			−1.18			1.11
	rv4-7	RM1136-RM273	0.08	rv6-6	RM276-RM314	0.04	4.67			−1.02			−0.85
	rv5-2	RM1054-RM87	0.10	rv7-10	RM418-RM560	0.00	5.75			−1.44			−0.96
	rv7b	RM478-RM18	0.00	rv8c	RM1308-RM264	0.04	7.97	1.15	0.55				−0.85
	rv7a	RM18-RM47	0.00	rv7-23	RM248-RM172	0.00	5.39	1.40					
	rv9b	RM410-RM215	0.16	rv11-7	RM229-RM21	0.00	8.70	0.78		−1.09	0.84		1.16
V	rv1-10	RM1231-RM1244	0.06	rv6-13	RM190-RM589	0.02	4.12			0.74			0.57
	rv1-26	RM579-RM583	0.02	rv2-7	RM1285-RM279	0.00	5.58			0.72			
	rv1-39	RM1247-RM1282	0.06	rv11-2	RM332-RM1124	0.02	8.33			−1.08			−0.75
	rv2-8	RM279-RM485	0.00	rv11-9	RM206-RM1233	0.00	5.42			−0.82			−0.67
	rv2-11	RM423-RM535	0.52	rv8c	RM1308-RM264	0.00	6.26		−0.61	0.74			0.56
	rv5-6	RM146-RM509	0.12	rv7-8	RM214-RM445	0.38	6.39			0.67			0.75
	rv5-9	RM548-RM267	0.02	rv6	RM345-RM412	0.02	4.51		0.57				
	rv7-1	RM51-RM1093	0.00	rv12a	RM491-RM101	0.18	6.18		1.02	0.89			
	rv8c	RM1308-RM264	0.04	rv9-4	RM342-RM409	0.78	5.43	−0.85			0.49		
	rv12a	RM491-RM101	0.12	rv12-7	RM270-RM1227	0.10	4.32	1.06			−0.68	−0.66	

**Table 9** Some important co-localizations of QTLs for root traits

Chromosome	Interval	QTLs	Trait
2	RM525-RM263	<i>brt2</i> , <i>m2d</i> , <i>rdw2c</i> , <i>rflw2c</i>	BRT, RN, RFW, RDW
6	RM345-RM412	<i>brt6b</i> , <i>m6b</i> , <i>rv6</i> , <i>rdw6</i>	BRT, RN, RV, RDW
4	RM349-RM1136	<i>mrl4b</i> , <i>rv4b</i> , <i>rdw9b</i>	MRL, RFW, RV
9	RM410-RM215	<i>mrl9</i> , <i>rdw9b</i> , <i>rv9b</i>	MRL, RV, RDW, RFW
7	RM432-RM346	<i>mrl7b</i> , <i>brt7a</i>	BRT, MRL
7	RM51-RM1093	<i>mrl7a</i> , <i>brt7b</i>	BRT, MRL
9	RM566-RM553	<i>mrl9b</i> , <i>brt9a</i>	BRT, MRL

**Table 10** The proportion of total additive QTLs contributed by IRAT109 or by Yuefu

Traits	Total QTLs	Contributed by IRAT109	Proportion (%)	Contributed by Yuefu	Proportion (%)
BRT	14	11	79	3	21
RN	13	5	39	8	61
MRL	14	10	71	4	29
RFW	11	9	82	2	18
RDW	12	6	50	6	50
RV	22	8	35	14	65

are selectively expressed at different stages. Only 2 QTLs for MRL (*mrl4a*, *mrl9a*) have been found continually expressed at four stages and might be related with root growth. Moriata et al. (1995) considered that a few weeks after germination an extensive post embryonic shoot-borne root system makes up the major backbone of root stock. These roots may elongate during all growth stages, and so some QTLs might be constantly expressed. On the other hand, no pair of epistatic QTLs was identified at two different stages. This might suggest that there are different epistatic QTLs systems in the different growth stages.

All these studies by Price et al (2002), Champoux et al. (1995) and ours confirmed that different QTL loci could be identified at different stages.

#### Co-localization and cluster distribution QTLs

Price et al. (2002) reported that in the same chromosomal region there were many QTLs affecting different root morphological characters. The results from our study showed that 20 of 89 additive QTLs were associated with more than two traits. The QTL at the interval RM525-RM263 was identified related with BRT, RN, RFW, and RDW, and another QTL at the interval RM1153-RM348 was associated with BRT, MRL and RV (Table 9). For the six root traits, only one pair of epistatic QTLs was related to two root traits, RFW and RV. The result indicated that

the epistatic effect was complex, and different root traits were controlled by different systems of epistatic effects.

Many researchers demonstrated that related QTLs can be spread on the entire genome (Price et al. 2002; Champoux et al. 1995; Yadav et al. 1997). In the present study, we identified a total of 89 QTLs distributed on the 12 chromosomes of rice although not proportionately. For example, there were 13 QTLs on chromosome 2, 14 QTLs on chromosome 4 and 10 QTLs on the lower part of chromosome 9, while chromosomes 10, 11, and 12 only had one or two QTL loci respectively. The QTLs for BRT and MRL were mainly located on chromosomes 1, 4, 7, and 9.

Furthermore, both parents contained favorable alleles for drought tolerance in rice, although IRAT109 had more. For BRT, 11 of the 14 additive QTLs at all growth stages were contributed by IRAT109 which accounted for 79%. For MRL, 10 of the 14 QTLs at all stages also came from IRAT109, accounting for 71%. Yuefu contributed for 61% of the favorable alleles for RN. The RI lines showed transgressive segregation for root traits mainly due to interactions between genes and genotype  $\times$  year (Table 10).

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